Traveling Waves in the Holling-Tanner Model
with Weak Diffusion

Anna Ghazaryan, Miami University
Vahagn Manukian, Miami University
Stephen Schecter, North Carolina State University

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Holling-Tanner prey-predator model

\[
U_\tau = rU \left(1 - \frac{U}{k}\right) - \frac{mU}{a + U} V
\]

\[
V_\tau = \rho V \left(1 - \frac{hV}{U}\right)
\]

- \(U\) is the population of the prey, \(V\) is the population of the predator,
- \(r\) is the intrinsic growth rate of the prey,
- \(k\) is the carrying capacity for the prey,
- Holling, 1959: the rate with which the predator captures the prey is normalized type II functional response \(\frac{mU}{a+U}\), \(m\) is the maximum rate of predation, \(a\) is proportional to the time required for the predator to search and find a prey;
- \(\rho\) is the intrinsic growth rate of the predator,
- Tanner, 1975: for the predator, carrying capacity is proportional to the size of the population of the prey, \(h\) is the number of prey required to support one predator at the nontrivial equilibrium.
Scaled Holling-Tanner model

\[ U_{\tau} = rU \left( 1 - \frac{U}{k} \right) - \frac{mU}{a + U} V \]

\[ V_{\tau} = \rho V \left( 1 - \frac{hV}{U} \right) \]

\[ t = r\tau, \quad u = U/k, \quad v = (m/kr)V, \quad \alpha = a/k, \quad s = \rho/r, \quad \beta = hr/m \]

\[ u_t = u(1 - u) - \frac{uv}{\alpha + u} \]

\[ v_t = \delta v \left( 1 - \frac{\beta v}{u} \right) \]

• \( u \) is the population of the prey,
• \( v \) is the population of the predator,
• \( \delta \) is the relative to the prey growth rate of predator,
• \( \beta \) is determined by the relative strength of the nonlinear coupled responses.
Nontrivial equilibrium

There is a unique equilibrium \((u_+, v_+)\) with both components positive:

\[
    u_+ = \frac{\beta(1 - \alpha) - 1 + \sqrt{(\beta(1 - \alpha) - 1)^2 + 4\alpha\beta^2}}{2\beta}, \quad v_+ = \frac{1}{\beta} u_+
\]

Previously known results:

- parameter regimes found where \((u_+, v_+)\) is globally stable (Hsu, Huang, 1995);
- existence of limit cycles studied (Gasull, Kooij, Torregrosa, 1997);
- Turing and Hopf bifurcations observed numerically (Banerjee, Banerjee, 2012; Sun, Zhang, Song, Jin, Li, 2012);
- conditions for Turing and Hopf bifurcations are derived, using a combination of analytical and numerical studies (Li, Jiang, Shi, 2013).
Global stability of the nontrivial equilibrium

Let \( \alpha_\pm = \frac{1}{4} (1 - \alpha - \delta) \pm \sqrt{(1 - \alpha - \delta)^2 - 8\alpha\delta}, \) \( \beta_\pm = \frac{\alpha_\pm}{(1-\alpha_\pm)(\alpha+\alpha_\pm)}. \)

Theorem [Hsu, Huang, 1995]. For the system

\[
\begin{align*}
    u_t &= u(1 - u) - \frac{uv}{\alpha + u} \\
    v_t &= \delta v \left( 1 - \frac{\beta v}{u} \right)
\end{align*}
\]

the equilibrium \((u_+, \frac{1}{\beta} u_+),\) where \( u_+ = \frac{\beta(1-\alpha)-1+\sqrt{(\beta(1-\alpha)-1)^2+4\alpha\beta^2}}{2\beta}, \) is globally asymptotically stable in the open 1st quadrant if one of the following holds

1. \( \alpha \geq 1; \)
2. \( \alpha < 1 \) and \( \alpha + \delta \geq 1; \)
3. \( \alpha + \delta < 1, (1 - \alpha - \delta)^2 - 8\alpha\delta > 0, \) and \( \beta > \beta_+; \)
4. \( \alpha + \delta < 1 \) and \( (1 - \alpha - \delta)^2 - 8\alpha\delta > 0, \beta \) sufficiently small and \( \beta < \beta_-; \)
5. \( \alpha + \delta < 1 \) and \( (1 - \alpha - \delta)^2 - 8\alpha\delta \leq 0. \)
Diffusive model

\[
\begin{align*}
    u_t &= d \Delta u + u(1 - u) - \frac{uv}{\alpha + u}, \quad x \in \mathbb{R}^n \\
    v_t &= \Delta v + \delta v \left(1 - \frac{\beta v}{u}\right)
\end{align*}
\]

Ducrot, 2013:

- studied the spreading speed of perturbation to \((u_+, v_+)\) is studied;
- proved that for a special type of initial conditions the spreading speed is as in KPP equation;
- initial conditions are the predator initially is compactly supported, the prey is well distributed.
Diffusive model: further scaling

We rewrite the diffusive system,

\[ u_t = D_u u_{xx} + u(1 - u) - \frac{uv}{\alpha + u}, \quad x \in \mathbb{R} \]
\[ v_t = D_v v_{xx} + \delta v \left( 1 - \frac{\beta v}{u} \right) \]

with \( D_u = \tilde{\epsilon} \) and \( \mu = D_v / D_u \)

\[ u_t = \tilde{\epsilon} u_{xx} + u(1 - u) - \frac{uv}{\alpha + u} \]
\[ v_t = \tilde{\epsilon} \mu v_{xx} + \delta v \left( 1 - \frac{\beta v}{u} \right) \]
Traveling waves

Reaction-diffusion systems on the spatially unbounded domain $\mathbb{R}$:

$$U_t = DU_{xx} + N(U)$$

Traveling waves: solutions which preserve their shape ($U_t = 0$) while propagating with a constant velocity

$$0 = DH_{\xi\xi} + cH_{\xi} + N(H)$$

Translation invariance $\implies \{H(\xi + a), a \in \mathbb{R}\}$
Traveling wave ODE

To capture traveling waves, introduce moving frame $\xi = x - ct, c > 0$,

$$u_t = \tilde{\epsilon} u_{\xi\xi} + cu_\xi + u(1-u) - \frac{uv}{\alpha + u}$$

$$v_t = \tilde{\epsilon} \mu v_{\xi\xi} + cv_\xi + \delta v \left(1 - \frac{\beta v}{u}\right)$$

Set $u_t = v_t = 0$,

$$0 = \tilde{\epsilon} u_{\xi\xi} + cu_\xi + u(1-u) - \frac{uv}{\alpha + u}$$

$$0 = \tilde{\epsilon} \mu v_{\xi\xi} + cv_\xi + \delta v \left(1 - \frac{\beta v}{u}\right)$$

Rescale $z = \xi/c$, denote $\epsilon = \tilde{\epsilon}/c^2$

$$0 = \epsilon u_{zz} + u_z + u(1-u) - \frac{uv}{\alpha + u}$$

$$0 = \epsilon \mu v_{zz} + v_z + \delta v \left(1 - \frac{\beta v}{u}\right)$$

We consider this system for $\epsilon \ll 1$
Slow-fast structure

\[
0 = \epsilon u_{zz} + u_z + u(1 - u) - \frac{uv}{\alpha + u}
\]

\[
0 = \epsilon \mu v_{zz} + v_z + \delta v \left(1 - \frac{\beta v}{u}\right)
\]

can be written as the first order slow-fast system with small parameter \(\epsilon \ll 1\)

\[
\frac{du}{d\xi} = \epsilon u_1
\]

\[
\frac{du_1}{d\xi} = -u_1 - u(1 - u) + \frac{uv}{\alpha + u}
\]

\[
\frac{dv}{d\xi} = \epsilon v_1
\]

\[
\frac{dv_1}{d\xi} = -\frac{1}{\mu} v_1 - \frac{\delta}{\mu} v \left(1 - \frac{\beta v}{u}\right)
\]
The equilibrium points

\[(u, v) = (1, 0, 0, 0), \quad (u, v) = (-\alpha, 0, 0, 0), \quad (u_\pm, 0, v_\pm, 0),\]

where

\[u_+ = \frac{\beta(1 - \alpha) - 1 + \sqrt{(\beta(1 - \alpha) - 1)^2 + 4\alpha\beta^2}}{2\beta}, \quad v_+ = \frac{1}{\beta}u_+.\]

and

\[u_- = \frac{\beta(1 - \alpha) - 1 - \sqrt{(\beta(1 - \alpha) - 1)^2 + 4\alpha\beta^2}}{2\beta}, \quad v_- = \frac{1}{\beta}u_.\]
The existence and geometry of traveling waves

The different types of traveling waves supported by diffusive Holling-Tanner Model
Singularly perturbed system: fast dynamics

Fast system

\[
\begin{align*}
\frac{du}{d\xi} &= \epsilon u_1 \\
\frac{du_1}{d\xi} &= -u_1 - u(1 - u) + \frac{uv}{\alpha + u} \\
\frac{dv}{d\xi} &= \epsilon v_1 \\
\frac{dv_1}{d\xi} &= -\frac{1}{\mu} v_1 - \frac{\delta}{\mu} v \left(1 - \frac{\beta v}{u}\right)
\end{align*}
\]

When \( \epsilon = 0 \), this system has a manifold of equilibria

\[
\mathcal{M}_0 = \left\{(u, u_1, v, v_1) : u_1 = \frac{uv}{\alpha + u} - u(1 - u), \ v_1 = \delta v \left(\frac{\beta v}{u} - 1\right), \ u > 0\right\}
\]

\( \mathcal{M}_0 \) is normally hyperbolic and attracting
Singularly perturbed system: slow dynamics

Slow system, $z = \epsilon \xi$

\[
\frac{du}{dz} = u_1
\]
\[
\epsilon \frac{du_1}{dz} = -u_1 - u(1 - u) + \frac{uv}{\alpha + u}
\]
\[
\frac{dv}{dz} = v_1
\]
\[
\epsilon \frac{dv_1}{dz} = -\frac{1}{\mu} v_1 - \frac{\delta}{\mu} v \left(1 - \frac{\beta v}{u}\right)
\]

When $\epsilon = 0$, the slow system has $\mathcal{M}_0$ as an invariant manifold.

The dynamics on $\mathcal{M}_0$ is given by

\[
\frac{du}{dz} = \frac{uv}{\alpha + u} - u(1 - u) = -\left(u(1 - u) - \frac{uv}{\alpha + u}\right)
\]
\[
\frac{dv}{dz} = \delta v \left(\frac{\beta v}{u} - 1\right) = -\delta v \left(1 - \frac{\beta v}{u}\right)
\]

-the same as the ode Holling-Tanner with $z = -t$
Traveling waves in singularly perturbed system

Strategy (use Fenichel Theory):

• Find a manifold $\mathcal{M}_0$ where the solutions of the system with $\epsilon = 0$ live.

• Show that $\mathcal{M}_0$ for small $\epsilon > 0$ perturbs to a unique invariant manifold $\mathcal{M}_\epsilon$ of the perturbed system (normal hyperbolicity of $\mathcal{M}_0$).

• Show that close to $\mathcal{M}_\epsilon$ no traveling wave can exist off $\mathcal{M}_\epsilon$ (if $\mathcal{M}_0$ attracting, then $\mathcal{M}_\epsilon$ is attracting too), so the dimensions of the system can be reduced by restricting the flow to $\mathcal{M}_\epsilon$.

• Show existence of waves (here heteroclinic solutions and closed orbits) on $\mathcal{M}_0$.

• Extend the information about the waves on $\mathcal{M}_0$ to $\mathcal{M}_\epsilon$ (transversality of intersection of the participating manifolds)

Need to show that there are traveling waves in

\[
\begin{align*}
\frac{du}{dz} &= \frac{uv}{\alpha + u} - u(1 - u) \\
\frac{dv}{dz} &= \delta v \left( \frac{\beta v}{u} - 1 \right)
\end{align*}
\]
Physical equilibria

\[(u, v) = (1, 0, 0, 0), \ (u_+, 0, v_+, 0);\]

\[
\begin{align*}
\frac{du}{dz} &= \frac{uv}{\alpha + u} - u(1 - u) \\
\frac{dv}{dz} &= \delta v \left(\frac{\beta v}{u} - 1\right)
\end{align*}
\]

we study interactions between \((u_+, v_+)\) and \((1, 0)\); dynamics driven by \((u_+, v_+)\)
Case I: $\beta > \frac{2(1-\alpha)}{(\alpha+1)^2}$

$A = (u_+, v_+)$ is strictly to the right of the vertex $V$

When $\delta > 0$, the equilibrium $A$ is unstable:

- there exist $\delta_-$ and $\delta_+$, $0 < \delta_- < \delta_+$, such that when $\delta \in (\delta_-, \delta_+)$, $A$ is an unstable focus,
- otherwise it is an unstable node.

Existence and Geometric Structure of Heteroclinic Orbits:

There is a heteroclinic connection from the equilibrium $B$ to the equilibrium $A$.

The orbit approaches $B$ along its stable manifold that corresponds to the negative eigenvalue $-\delta$. If $\delta \in (\delta_-, \delta_+)$ then the orbit leaves the equilibrium $A$ along its weak unstable manifold, otherwise the corresponding front solution has an oscillatory tail.
Singular front at $\delta = \infty$

$$\frac{du}{dx} = \frac{1}{\delta} \left( \frac{uv}{\alpha + u} - u(1-u) \right), \quad z = \frac{1}{\delta} x$$

$$\frac{dv}{dx} = v \left( \frac{\beta v}{u} - 1 \right)$$

Singular solution, $\delta = \infty$; Perturbd solution, $\delta \gg 1$
Singular front at $\delta = 0$

When $\delta = 0$, the limiting system (fast system) reads

$$u' = \frac{uv}{\alpha + u} - u(1 - u)$$

$$v' = 0$$

Singular solution, $\delta = 0$  

Perturbed solution, $\delta \ll 1$
Rotation vector fields

\[
\begin{pmatrix}
\frac{du}{dz} \\
\frac{dv}{dz}
\end{pmatrix}
= \begin{pmatrix}
\frac{uv}{\alpha+u} - u(1-u) \\
\delta v \left( \frac{\beta v}{u} - 1 \right)
\end{pmatrix}
= \begin{pmatrix}
f_1(u, v) \\
f_2(u, v)
\end{pmatrix}
= F(u, v)
\]

The nullclines and the equilibria are independent of \(\delta\).

The angle between the \(u\)-axis and \(F(u, v)\) is \(\Theta(u, v) = \tan^{-1} \frac{\delta f_2(u, v)}{f_1(u, v)}\).

\[
\frac{\partial \Theta}{\partial \delta} = \frac{f_1 \frac{\partial (\delta f_2)}{\partial \delta} - \delta f_2 \frac{\partial f_1}{\partial \delta}}{f_1^2 + (\delta f_2)^2} = \frac{v}{u+\alpha} \left( \frac{(1-u)((\alpha+u) - v)(u-\beta v)}{(u(1-u) - \frac{uv}{\alpha+u})^2 + (\delta v(1-\frac{\beta v}{u}))^2} \right) < 0
\]

in the region \(S\) which is the region bounded from the left and right by the two singular waves and by \(v = (1/\beta)u\) from above.

As \(\delta\) increases the vector field in that region rotates clockwise.

As \(\delta\) decreases, the segments of saddle separatrices which are in \(S\)

(a) move monotonically clockwise along transversals (i.e. along each sufficiently small circle centered at the saddle point \(B\)) from the initial position to the final position which is the orbit that corresponds to \(\delta = 0\);

(b) never self-intersect, i.e. \(W^s(B)(\delta^*) \cap W^s(B)(\delta^{**}) = \emptyset\), for \(\delta^* \neq \delta^{**}\).

As \(\delta\) decreases, the orbit at \(\delta = \infty\) leaves \(S\) through the side \(v = (1/\beta)u\).
Geometry of the waves

- a) \( \delta \in (0, \delta_-) \)
- b) \( \delta \in (\delta_-, \delta_+) \)
- c) \( \delta \in (\delta_+, +\infty) \)

Schematic representation of the heteroclinic orbits on the slow manifold.
Existence of fronts, $\beta > \frac{2(1-\alpha)}{(\alpha+1)^2}$

**Theorem.** Given $\beta, \mu, \delta > 0$, and $\beta > \frac{2(1-\alpha)}{(\alpha+1)^2}$, there exists $\epsilon^* = \epsilon^*(\delta, \alpha, \beta, \mu) > 0$ such that for any $\epsilon < \epsilon^*$, there is a unique up to translation traveling front $(u(z, t), v(z, t)) = (u(z), v(z))$ that satisfies the boundary conditions

$$\lim_{z \to +\infty} (u(z), v(z)) = (1, 0),$$

$$\lim_{z \to -\infty} (u(z), v(z)) = (u_+, v_+).$$

Moreover, the convergence to the rest state $B$ is always monotone, while there exist $\delta_-$ and $\delta_+ (0 < \delta_- < \delta_+)$ independent of $\epsilon$ such that for each $\delta$ there exists $\epsilon^{**} \leq \epsilon^*$ such that for every $\epsilon < \epsilon^{**}$ the convergence of the traveling fronts to the rest state $A$ is oscillatory if $\delta \in (\delta_-, \delta_+)$ and monotone if $\delta \in (0, \delta_-) \cup (\delta_+, \infty)$.

$$0 = \epsilon u_{zz} + u_z + u(1 - u) - \frac{uv}{\alpha + u}$$

$$0 = \epsilon \mu v_{zz} + v_z + \delta v \left(1 - \frac{\beta v}{u}\right)$$
Case II: $\beta < \frac{2(1-\alpha)}{(\alpha+1)^2}$

$A$ is strictly to the left of the vertex $V$

In the reduced system, $B = (1, 0)$ is a saddle.

About $A$: there exist $\delta_1, \delta_h, \delta_2$, such that $0 < \delta_1 < \delta_h < \delta_2$ and

- $A$ is a stable node when $\delta \in (0, \delta_1)$,
- $A$ is a stable focus when $\delta \in (\delta_1, \delta_h)$,
- $\delta_h = -\frac{f_1}{f_2}u$ is the Hopf bifurcation point,
- $A$ is an unstable focus when $\delta \in (\delta_h, \delta_2)$,
- $A$ is an unstable node when $\delta \in (\delta_2, \infty)$. 
Fronts in Case II: $\delta$ at and near $\infty$

\[
\frac{du}{dz} = \frac{1}{\delta} \left( \frac{uv}{\alpha + u} - u(1 - u) \right)
\]

\[
\frac{dv}{dz} = v \left( \frac{\beta v}{u} - 1 \right)
\]

Singular solution, $\delta = \infty$  

Perturbed solution, $\delta \gg 1$

For $\delta > 1 - \alpha$, $A$ is globally unstable.

Stable manifold of $B$ rotates counterclockwise until it meets the parabolic nullcline.
Case II: Existence of fronts

Theorem. Given $\beta$, $\mu$, $\delta$ sufficiently large, and $\beta < \frac{2(1-\alpha)}{(\alpha+1)^2}$, there exists $\epsilon^* = \epsilon^*(\delta, \alpha, \beta, \mu) > 0$ such that for any $\epsilon < \epsilon^*$, there is a unique up to translation traveling front $(u(z, t), v(z, t)) = (u(z), v(z))$ that satisfies the boundary conditions

$$\lim_{z \to +\infty} (u(z), v(z)) = (1, 0),$$

$$\lim_{z \to -\infty} (u(z), v(z)) = (u_+, v_+).$$

The convergence to the rest state $B$ is always monotone. Moreover, there exist $\delta_+ > 0$ such that the following is true. For each large $\delta > 0$ with $\delta \neq \delta_+$, there exists a positive $\epsilon^{**} \leq \epsilon^*$ such that for every $0 < \epsilon < \epsilon^{**}$, the convergence of the traveling front to $A$ is oscillatory if $\delta < \delta_+$ and monotone if $\delta > \delta_+$. 
The case of $A$ to the left of the vertex and small $\delta$.

Use alternative formulation to use polynomial vector fields techniques:

On the set $\{(u, v), u > 0, \ v \geq 0\}$, the system

\[
\frac{du}{dz} = \frac{uv}{\alpha + u} - u(1 - u)
\]

\[
\frac{dv}{dz} = \delta v \left( \frac{\beta v}{u} - 1 \right)
\]

is topologically equivalent to

\[
u' = -u^2 ((1 - u)(\alpha + u) - v)
\]

\[
v' = -\delta v(\alpha + u) (u - \beta v)
\]

by means of the coordinate transformation

\[
\zeta = \int_0^\xi \frac{1}{u(\alpha + u)} \, ds
\]
Singular closed orbit $S$ for $\delta = 0$

$$u' = -u^2 ((1 - u)(\alpha + u) - v) = u^2 h_1(u, v)$$

$$v' = -\delta v(\alpha + u)(u - \beta v) = \delta h_2(u, v)$$

When $\delta = 0$,

$$u' = -u^2 ((1 - u)(\alpha + u) - v)$$

$$v' = 0$$

Singular flow, $\delta = 0$  
Singular closed orbit $S$
Relaxation oscillations for small $\delta$

\[
h_1(u, v) = -((1 - u)(\alpha + u) - v)
\]

\[
h_2(u, v) = -v(\alpha + u)(u - \beta v)
\]

Position of $v_0^*$: let

\[
G(v_0) = \int_{v_0}^{v_0^*} \frac{h_1(0, v)}{h_2(0, v)} \, dv
\]

There is a unique $0 < v_0^* < \alpha$ such that $G(v_0^*) = 0$

**Theorem.** For a fixed $(\alpha, \beta)$ as in Case II, there is a neighborhood $U$ of $S$ such that for small $\delta > 0$, there is a unique closed orbit $S_\delta$ in $U$. $S_\delta$ is hyperbolically repelling and approaches $S$ as $\delta \to 0$. (Follows from [De Maesschalck, Schecter, The entry-exit function and gsp, 2016])

**Theorem.** Assume $(\alpha, \beta)$ is in Case II, $\delta > 0$ is sufficiently small, and $\mu > 0$. Then there exists $\epsilon^* = \epsilon^*(\alpha, \beta, \delta, \mu) > 0$ such that for any positive $\epsilon < \epsilon^*$, there is a periodic solution $(u, v)$ of the original traveling wave system.
Hopf bifurcation

$A$ is strictly to the left of the vertex $V$, $\delta_h = \frac{-f_1u}{f_2v}$ is the Hopf bifurcation point.

When $A$ is close to the vertex, the closed orbits are repelling like the relaxation oscillator (by Lyapunov number calculation).
Closed orbits

$A$ is strictly to the left of the vertex $V$, $\delta_h = \frac{-f_1u}{f_2v}$ is the Hopf bifurcation point

When $A$ is not close to the vertex, the closed orbits are attracting
We imply that there is a value of $\delta$, $0 < \delta < \delta_h$, for which multiple periodic orbits